PROC. BIOL. SOC. WASH.
92(3), 1979, pp. 551–571

A SYNOPSIS OF THE MILLIPED GENUS *CAMBALA*, WITH A DESCRIPTION OF *C. MINOR* BOLLMAN (SPIROSTREPTIDA: CAMBALIDAE)

Rowland M. Shelley

Abstract.—The spirostreptid milliped genus *Cambala* is summarized; *annulata* (Say), *minor* Bollman, *texana* Loomis, *ochra* Chamberlin, *speobia* (Chamberlin), *washingtonensis* Causey, and *hubrichti* Hoffman are recognized as valid species. The remaining six nominal species are relegated to appropriate synonymies. *Cambala minor* is described and illustrated for the first time, and the posterior gonopods of all species except *washingtonensis* are compared, to establish their identities. The latter is known only from females, and its identity is still obscure. The occurrence of *Cambala* in the Pacific northwest is confirmed, as authentic specimens have been collected in southwestern Oregon, and the range of *annulata* is extended to the vicinity of Pittsburgh, Pennsylvania. *Cambala* is widespread and common in unglaciated portions of the eastern United States from southwestern Pennsylvania and southern Illinois to the Gulf Coastal Plain, ranging westward to the Edwards Plateau region of west Texas and adjoining areas.

The milliped genus *Cambala* is the only representative of the family Cambalidae in the eastern United States. In the southern Appalachian Mountains and southern Atlantic States, individuals of *C. annulata* (Say) and *C. hubrichti* Hoffman are a dominant element of the litter fauna, being more prevalent in the cooler months of spring and fall. The distinctions between these two large species were detailed by Hoffman (1958), who also clarified their nomenclature. The situation is quite different in the Cumberland Plateau and midwestern states, however. Small to moderate sized cambaloids range southwestward into Texas and adjacent areas and are common in the surface and cave faunas, but their identities are uncertain and their nomenclature, confusing. Miscellaneous records exist in a number of papers, but none can be considered reliable. The only comprehensive treatment is that of Loomis (1938), but several additional species have been described, and there have been other nomenclatorial changes. Today, *Cambala* is comprised of the following 12 species, one of which is divided into two subspecies. I here recognize only seven of these as valid, the others placed in synonymy as indicated. In the ensuing discussions they will be referred to only by the specific or specific and subspecific names.

annulata (Say, 1821)
minor Bollman, 1888
  arkansana Chamberlin, 1942
  cara Causey, 1953
texana Loomis, 1938
ochra Chamberlin, 1942
  saltillona Chamberlin, 1943
  loomisi (Hoffman, 1956)
speobia (Chamberlin, 1952)
  reddelli reddelli Causey, 1964
  reddelli inornatus Causey, 1964
washingtonensis Causey, 1954
hubrichti Hoffman, 1958

The major difficulty in the taxonomy of *Cambala* has been uncertainty about the identity of *minor,* which was originally described as a subspecies of *annulata* by Bollman (1888a). He published no illustrations, as he never did in any of his papers, and reported no diagnostic characters. His only comment was that the new form was "similar to *C. annulata,* but much smaller and of a yellowish-brown shade." Loomis (1938) missed a golden opportunity to resolve the problem when, in elevating *minor* to a full species, he neglected to examine the type specimens and based his conclusion entirely on the meaningless drawing of Williams and Hefner (1928) for a form from Ohio. Loomis' action was correct, though risky without viewing the type material, but he did not clarify the identity of the species. All subsequent species of *Cambala* have likewise been described without anyone's examing Bollman's types, which have rested all these years at the U.S. National Museum. Consequently, synonymies have developed, and the confusion is such that the only species which can be accurately identified today are *annulata* and *hubrichti* due to Hoffman's treatment (1958).

My interest in this problem developed after receiving several shipments of midwestern cambaloids for identification. After examining the types of *Cambala annulata minor,* it was immediately obvious that *cara,* for which an illustration of the posterior gonopod had been published (Causey, 1953), was a synonym. Since the type locality of *arkansana* is only a few counties east of that of *cara,* it seemed likely that this species too was identical to *minor.* The question thus arose as to how many more synonymies existed among the 12 nominal species of *Cambala.* Causey (1964) disposed of *caeca* Loomis and *captiosa* Causey by bringing them under *speobia,* but it seemed that the genus could be reduced still further. Consequently, I have undertaken a review of *Cambala* to clarify the nomenclature and provide, for the first time, a definitive description of *minor.* Types of all species including *caeca* and *captiosa* have been examined except that of *washingtonensis,*

which is absent from its published repository, the American Museum of Natural History (AMNH). Chamberlin and Hoffman (1958) suggested that this species was probably not congeneric with the others, but I have seen crested cambaloids from Oregon at the AMNH that closely resemble the eastern species externally and key out to *Cambala* in Loomis' key (1938). They resemble *speobia* in the configuration of the posterior gonopods, and suggest that *washingtonensis* may be a valid species of *Cambala* after all.

The results of this study indicate that there are only six unquestionably valid species of *Cambala*; *washingtonensis* is here treated as valid but may prove to be a synonym of *speobia*. Since *washingtonensis* was based on a female, topotypical males are needed to resolve its status. Synonymies, type localities, and known ranges are listed herein for each species of *Cambala,* along with miscellaneous comments and illustrations of the posterior gonopods. The configuration of the posterior gonopod, particularly the coxal process, seems the only reliable character for identifications. Overall size is of some value, and there are three distinct classes, with *minor* and *ochra* being intermediate between *annulata* and *hubrichti,* the largest species, and *speobia* and *texana,* the smallest. *Cambala annulata* and *hubrichti* can be separated by somatic features (Hoffman, 1958), but I have been unable to discern external differences between the other species.

The species reported herein are those that have been placed in *Cambala* by past authors. No new species were discovered among the hundreds of specimens examined, and it seems unlikely that any more exist east of the Mississippi River. I have not attempted to deal here with the larger issue of distinctions between the various Nearctic cambaloid genera or redefinition of the genus *Cambala*. Shear (1969) suggested that both *Mexicambala* and *Troglocambala* should be regarded as synonyms of *Cambala,* but Causey (1971) asserted that the former was distinct based upon "well defined somatic and sexual characters." Shear later (1973) agreed with this assessment. I have evaluated *Troglocambala* and concur that it is not a valid genus. Some of the distinguishing characters of *Troglocambala* are insignificant, whereas others vary between individuals. The reduced ornamentation of the dorsum, for example, is found frequently in *Cambala,* which suggests that some of the "smoother" western genera may not be valid. A critical review of all Nearctic cambaloid genera is badly needed and should receive a high priority when future revisions of North American diplopods are considered.

Acknowledgments

I am grateful to the following curators for loan of type specimens in their care: Ralph E. Crabill, Jr., U.S. National Museum; Norman I. Platnick, American Museum of Natural History; and Eric H. Smith, Field Museum

of Natural History. Access to the types in the Chamberlin collection was kindly provided by Richard L. Hoffman, who also loaned material in his personal collection and reviewed an early draft of the manuscript. Specimens in the Florida State Collection of Arthropods were studied with permission of Howard V. Weems, Jr., and those in the Museum of Comparative Zoology, Harvard University, through the courtesy of Herbert W. Levi. I also thank William A. Shear and Charles P. Withrow for loan of cambaloids in their collections. This study was aided by financial assistance from the National Science Foundation, Grant No. DEB-7702596.

Acronyms cited in the text to denote the sources of preserved study material of *minor* are as follows: AMNH—American Museum of Natural History, New York, NY; FSCA—Florida State Collection of Arthropods, Gainesville, FL; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MS; NCSM—North Carolina State Museum, Raleigh, NC; RLH—Private collection of Richard L. Hoffman, Radford, VA; RVC—Private collection of the late Ralph V. Chamberlin, now being accessioned by the U.S. National Museum; WAS—Private collection of William A. Shear, Hampden-Sydney, VA.

Genus *Cambala* Gray

Cambala Gray, 1832:784, pl. 135, figs. 2, 2a–c. Bollman, 1887:38; 1893:120. McNeill, 1888:10. Williams and Hefner, 1928:123. Loomis, 1938:36–37. Causey, 1953:155; 1959a:234; 1964:237–238; 1971:273. Chamberlin and Hoffman, 1958:173.
Eclytus (nec Holmgren, 1855) Chamberlin, 1952a:10–11.
Eclomus Chamberlin, 1952b:71. Chamberlin and Hoffman, 1958:175.
Troglocambala Hoffman, 1956:9–10.

Type-species.—Of *Cambala, C. lactaria* Gray, 1832 (= *Julus annulatus* Say, 1821), by monotypy; of *Eclomus, E. speobius* Chamberlin, 1952b, by original designation; of *Troglocambala, T. loomisi* Hoffman, 1956, by original designation.

Species.—Seven, distinguishable by the configuration of the anterior coxal lobes of the posterior male gonopods, as shown in Figs. 5–10. Hoffman (1958) produced a couplet based on somatic and gonopodal characters separating *annulata* and *hubrichti,* the two largest species, which are sympatric in the southern Appalachians. However, I have been unable to detect any reliable crest or other somatic characters which can separate all the species of *Cambala*.

Range.—The distribution of *Cambala* has never been precisely defined. Loomis (1938) stated that it was the most widespread of the American cambaloid genera, occurring in many of the eastern states, Texas, and Arkansas. Causey (1964) described the range as being the United States from western

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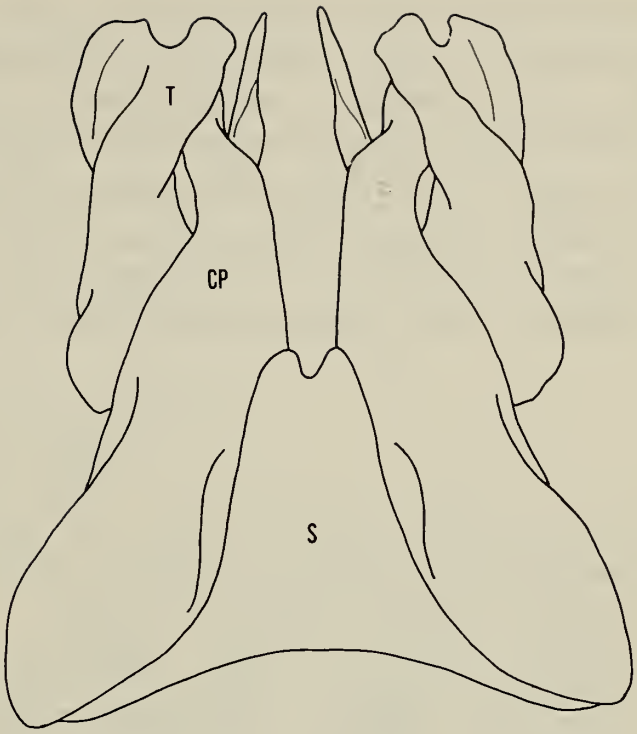

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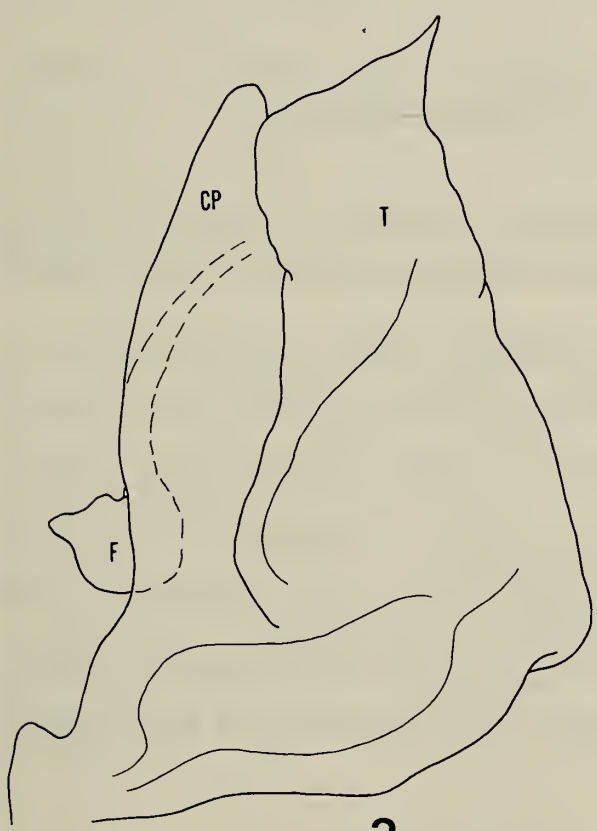

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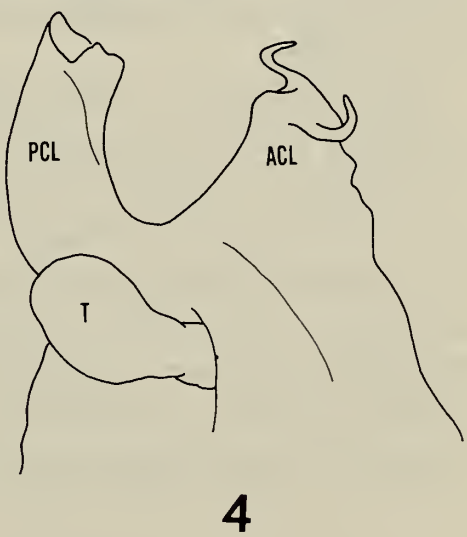

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Figs. 1–4. *Cambala minor* lectotype. **1,** left first leg, lateral view. **2,** anterior gonopods, cephalic view. **3,** left anterior gonopod, lateral view. **4,** left posterior gonopod, lateral view. **ACL**, Anterior Coxal Lobe; **CP**, Coxal Plate; **F**, Flagellum; **PCL**, Posterior Coxal Lobe; **S**, Sternum; **T**, Telopodite. Scale line = 0.1 mm for figs. 1, 3, and 4; 0.125 mm for fig. 2.

Washington and northern Idaho to the Atlantic Coast, with a center of abundance in the Appalachian Mountains. As shown in the inset map of Fig. 13, *Cambala* is widespread in unglaciated portions of the eastern United States from southwestern Pennsylvania-southern Illinois south to the Gulf Coastal Plain and northern Florida. Westward, the range extends through Louisiana and Arkansas to New Mexico and the Edwards Plateau region of west Texas. Its occurrence in the Pacific northwest can now be confirmed, due to the material from Oregon at the AMNH.

Cambala annulata (Say)
Figs. 5, 11

Julus annulatus Say, 1821:103–104. Bollman, 1893:145.
Cambala lactaria Gray, 1832:784, pl. 135, figs. 2, 2a–c.
Cambala lactarius Gervais, 1837:48.
Cambala annulata Cope, 1869:181. Bollman, 1887:38–39; 1888b:339. McNeill, 1888:10. Chamberlin, 1918:24; 1947:58; 1952c:30. Brimley, 1938:498. Hoffman, 1958:91–92. Wray, 1967:158. Shelley, 1978:54–56, fig. 44.
Cambala cristula Loomis, 1938:39, fig. 12; 1939:168; 1943:390. Causey, 1953:156; 1959a:234. Chamberlin and Hoffman, 1958:174.
Spirobolus annulatus Wood, 1865:212.

Type locality.—Southeastern United States, probably in Atlantic Coastal Plain between Charleston, South Carolina, and Jacksonville, Florida (Hoffman, 1958).

Range (Fig. 11).—The range cited by Hoffman (1958), central Virginia to northern Florida and inland from unglaciated portions of Ohio and Indiana to Alabama, can now be expanded to include southwestern Pennsylvania. Specimens from Pittsburgh, Allegheny Co., are present in the MCZ collection. Several males and females from Bryn Mawr, Montgomery Co., are available at the FSCA, but the complete absence of any specimens from Maryland, District of Columbia, and northern Virginia indicate that this is surely an error. In all the years O. F. Cook was at the USNM he never found one individual in the DC area. Additional material from Bryn Mawr

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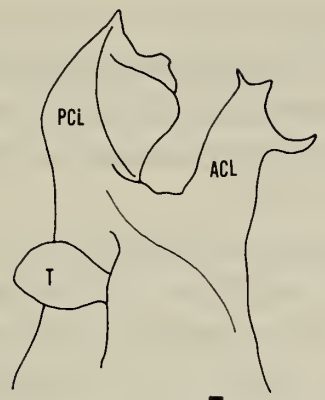
Figs. 5–10. Left posterior gonopods of six species of *Cambala*, lateral views, setation omitted. **5**, *annulata*, specimen from Chatham Co., NC. **6**, *hubrichti*, specimen from Cocke Co., TN. **7**, *minor* lectotype, specimen from Bloomington, Monroe Co., IN. **8**, *ochra*, specimen from Hart Co., KY. **9**, *speobia*, specimen from Williamson Co., TX. **10**, *texana* holotype, specimen from Nacogdoches Co., TX. **ACL**, Anterior Coxal Lobe; **PCL**, Posterior Coxal Lobe; **T**, Telopodite. Scale lines apply to the figures on either side and = 0.5 mm for figs. 5–6, and 0.1 mm for figs. 7–8 and 9–10.



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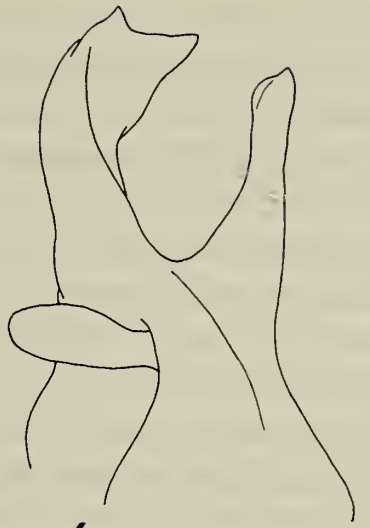

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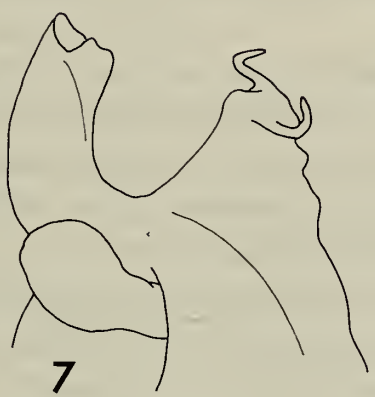

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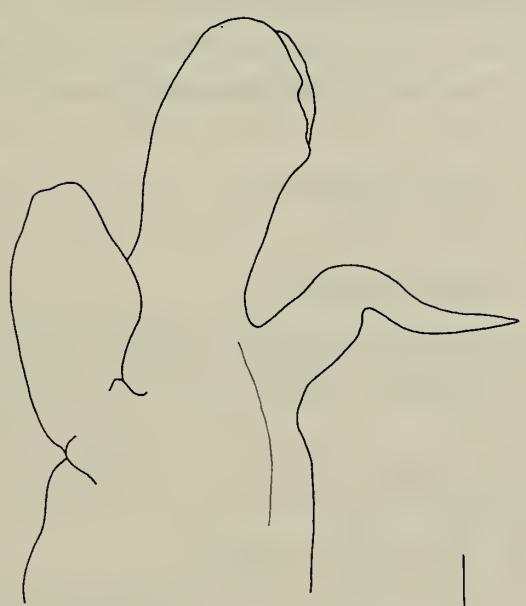

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is needed before this record can be given any credence. The map (Fig. 11) encompasses all known locality records including those amassed since Hoffman's account (1958). The record of Chamberlin (1952a) from Asheville, Buncombe Co., North Carolina, could be either *annulata* or *hubrichti,* as I have collected both species from near this city.

Ecology.—Hoffman (1958), reporting on montane specimens of *annulata,* stated that individuals tended to be rather secretive and occurred in the deepest levels of humus or burrows of small mammals. The most popular habitat was moist areas in dry upland oak woods, but the species was occasionally found under partly buried logs and rotting stumps in dry sites. In eastern Piedmont North Carolina, *annulata* is more prevalent in the cooler weather of spring and fall and is common in deep leaf piles. The milliped is hard to find in the summer, however, and only one juvenile has been collected in August (Shelley, 1978).

Remarks.—Although I have not conducted an exhaustive study of the gonopods of *annulata,* they do seem to be quite homogeneous throughout the range. Therefore, it seems that Loomis' name, *cristula,* relegated to the synonymy by Hoffman (1958), is destined to remain there and not be resurrected for a geographic race in the Appalachian region.

Loomis (1943) reported an anomalous male from Jackson Co., Florida, which had two sets of apparently normal gonopods in typical apertures on segments 7 and 8. The location of this individual is unknown; I could not find it at the MCZ in August 1978, and this was the repository of most of the material on which his paper was based. Assuming Loomis' description is correct, this would be an example of heteromorphosis in addition to those I reported in 1977 and the only abnormal non-polydesmid known from North America.

Cambala minor Bollman
Figs. 1–4, 7, 12

Cambala annulata minor Bollman, 1888a:404–405.
Cambala minor Loomis, 1938:40. Chamberlin and Hoffman, 1958:174–175.
?*Cambala minor* Loomis, 1943:390. Causey, 1959a:234–235; 1963:79. Shear, 1969:135, fig. 1.
Cambala annulata (nec Say, 1821) Bollman, 1887:38–39; 1888b:339; 1888c, 1. Williams and Hefner, 1928:123, fig. 17B.
?*Cambala annulata* (nec Say, 1821) McNeill, 1888:10.
Cambala arkansana Chamberlin, 1942:3, figs. 2–3. Chamberlin and Hoffman, 1958:174. NEW SYNONYMY.
Cambala cara Causey, 1953:156, figs. 13–14. Chamberlin and Hoffman, 1958:174. NEW SYNONYMY.

Type specimens.—Bollman deposited a type series of two males and eleven females in the U. S. National Museum without designating a holotype.

A male was selected from these syntypes by Dr. Hoffman on 12 January 1957, and I officially designate it the lectotype of *Cambala annulata minor*. The type series was collected by C. H. Bollman from Bloomington, Monroe Co., Indiana, on an unspecified date, which was probably between 1885 and 1887.

Diagnosis.—A moderate sized species of *Cambala* distinguished by two uncate projections from the anterior coxal lobe of the posterior gonopod and by the distal concavity on the anterior edge of the posterior coxal lobe of this structure.

Lectotype.—Body long and slender, slightly narrower in neck region, with approximately 64 segments, segment 4 and last two segments without legs. Specimen tightly coiled, length unmeasurable, width 1.5 mm.

Color yellowish as noted by Bollman (1888b), caudal portions of dorsal crests slightly brownish.

Head with 6 ocelli in linear row on each side. Relative lengths of antennomeres: $2 = 3 > 6 > 5 = 4 > 1 > 7$.

Collum smooth and shiny, minutely granular, extending forward to back edge of ocellar row; subequal in length to next two segments. Low dorsal crests beginning on segment 2, becoming progressively larger and reaching maximum height on segment 5, terminating on penultimate segment; 4 dorsal crests between peritremata; approximately 11–12 crests laterally on sides of body, becoming thinner and less distinct ventrally. Peritremata beginning on segment 5 and continuing to antepenultimate segment, pear shaped, posterior portion subequal in width and height to dorsal crests, anterior portion about twice as broad and slightly more elevated; pore in center of anterior portion. Surface between crests smooth, minutely granular.

Epiproct broadly rounded, not extending beyond valves; paraprocts reentrant; hypoproct short and very broad, margin straight, lateral corners covered by small processes emerging from beneath terminal segment.

First legs (Fig. 1) short, 6 segments, proximal two segments widest, terminal claw absent.

Anterior gonopods (Figs. 2–3) separated by high, apically divided sternum, coxal plates curving distad behind telopodites, apically divided and expanded caudad into thin laminae; telopodites apically divided with lateral portion moderately expanded caudad; flagella arising at posterobasal edges of laminae of coxal plates. Posterior gonopods (Figs. 4, 7) with anterior coxal lobes terminating in two short uncate projections arising on medial and lateral sides; posterior lobes with typical hamate setae, blunt, distal concavity on anterior edge; telopodites extending slightly beyond caudal margin of gonopod.

Paralectotypes.—Although the gonopods are fully developed, the male paralectotype is not fully grown, with only 50 segments, the last five legless. The dimensions are length 22.1 mm, width 1.3 mm. The most conspicuous

variation among the type specimens is the size of the crests, which are much sharper and more distinct on the paralectotypes than on the lectotype. The latter has the lowest and most rounded crests of any specimen of *C. minor* I have seen.

Variation.—There is some color variation in the species. After 90 years in alcohol, the type specimens are still yellowish, but other specimens are gray, approximately the same color as *annulata*.

Legs 4–7 were damaged in the dissections of both male type specimens, and the following observations were taken from the male from Greene Co., OH, whose gonopods are identical to those of the lectotype. Legs 4–5 are normal, but the femora of legs 6–7 have small lobes on the ventral sides. The lobe on leg 6 is slightly larger.

The anterior process of the posterior gonopod varies with respect to the height of the flattened portion between the two hooked projections. On the lectotype it is low, resulting in two distinct hooked projections. On some specimens, however, it is higher and produced into a blunt tooth anteriad. The two hooked projections always point ventrad, except for a male from Jeff Davis Co., Miss., in which they curve mediad to the base of the process.

Ecology.—Cambala minor is a troglophilic milliped which can live and reproduce in epigean and subterranean habitats. In Arkansas Causey (1953) recorded it from several surface habitats including pine forests near creeks, dry oak and oak-hickory hillsides, and under driftwood on a marshy creek bank. Causey (1959a) reported finding it on bat, rat, and raccoon dung, wet gravel, and in humus in the entrance and twilight zones of caves in the Cumberland Plateau, but some of these may have been specimens of *ochra* instead.

Distribution (Fig. 12).—*Cambala minor* occurs widely in the east-central region of the United States, from the Ridge and Valley Province of western Virginia to the Ozark region of Arkansas, north to south-central (unglaciated) Ohio-Indiana and south to the Gulf Coastal Plain. Specimens have been examined as follows; "female only" samples are reported from areas where *minor* is the only small cambaloid known to occur.

Virginia: Alleghany Co., McElwee's Cave, ♀ Feb. 1950, R. L. Hoffman (RLH). Tazewell Co., Burke's Garden, ♀, 20 April 1957, R. L. Hoffman (RLH). Bath Co., Clark's Cave, ♂, 15 April 1960, J. R. Holsinger (FSCA). Augusta Co., Glade Cave, juv. ♂, ♀, 1 April 1960, J. R. Holsinger (FSCA); and Cane Hill Cave, 2 ♂, Nov. 1961, J. R. Holsinger (FSCA). Washington Co., Fraley's Cave, Wyndale, ♀, 6 December 1960, C. W. Greever (FSCA).

West Virginia: Pendleton Co., 1 mi. NE Mouth of Seneca, ♀, 30 May 1952, L. Hubricht (RLH). Greenbriar Co., Higgenbotham Cave, ♀, 11 April 1957, T. C. Barr and D. F. Black (RLH); Arbuckle School Cave, Max-

wellton, ♂, ♀, S. B. Peck, 26 June 1968 (WAS); Ludington Cave, 2000′ from Bell entrance, ♂, 2 October 1965, J. M. Rutherford (FSCA): and Rapps Cave, ♂, ♀, 13 May 1962, J. R. Holsinger (FSCA). McDowell Co., Windmill Gap near McComas, ♀, 15 April 1973, W. M. McKenzie (WAS).

Kentucky: Carter Co., along U. S. hwy. 460, 5 mi. W Grayson, ♀, 22 April 1960, R. L. Hoffman and J. G. Barker (RLH). Bell Co., Pine Mountain State Park, wildflower garden, ♂, 4 ♀, Feb. 1976, J. K. Ettman (NCSM A797). Clark Co., along Boone's Creek near Athens, 4 ♂, 4 ♀, 11–23 October 1976, T. C. Barr and J. Reddell (FSCA). Hart Co., Rosebury near Cane Cr., 3 ♂, 5 October 1957, L. Hubricht (RLH). Barren Co., Short Cave Sink, 2.2 mi. NW Park City, 4 ♂, 3 ♀, 27 April 1975, L. Hubricht (RLH). Edmonson Co., Green R. floodplain near Styx R., 9 ♂, several fragmented ♀ ♀, 20 October 1956, L. Hubricht (RLH).

Ohio: Greene Co., Yellow Springs, Glen Helen, ♂, ♀, 16 November 1968, A. A. Weaver (WAS).

Indiana: Jefferson Co., 3.5 mi. W Madison, 4 ♂, 5 ♀, 10 March 1956, L. Hubricht (RLH); and Wilson Cave, ♂, 9 August 1964, T. C. Barr and S. B. Peck (FSCA). Harrison Co., King's Cave, 3.5 mi. E Corydon, juv. ♂, ♀, L. Hubricht (RLH). Crawford Co., hillside near Wyandotte Cave, ♂, ♀, 26 October 1958, T. C. Barr (FSCA). Monroe Co., Bloomington, 2 ♂, 11 ♀, date unknown, C. H. Bollman (USNM) TYPE LOCALITY. Posey Co., upland woods 2.4 mi. N Solitude, 2 ♂, 2 ♀, L. Hubricht (RLH).

Illinois: Union Co., 2.5 mi. NE Alto Pass, Union Point Cave, ♂, 18 August 1968, S. B. Peck (WAS). Monroe Co., Saltpeter Cave, 2 ♀, 25 June 1965, S. B. Peck (FSCA); and Monroe Cave, Fults, ♀, 23 April 1966, S. B. Peck (FSCA). St. Clair Co., Falling Spring, ♀, 13 June 1966, S. B. Peck (FSCA). Franklin Co., Zeiglar, 3 ♂, ♀, 20 April 1930, R. V. Chamberlin (FSCA).

Missouri: Perry Co., 3 mi. SE Perryville, Lost Cave and Found Cave, 2 ♂, 2 ♀, 29 December 1970, D. A. Easterla (WAS); Lost Cave ♂, ♀, 3 November 1963, R. Stattel (FSCA). Taney Co., Tumbling Creek Cave near Protem, ♂, 10 January 1978, M. W. Fletcher (FSCA).

Arkansas: Benton Co., Cave Springs, ♂, ♀, 6 April 1951, B. L. Tatum (AMNH). Washington Co., 15 mi. SW Prairie Grove, ♂, 3 ♀, 15 March 1958, M. Hite (RLH); Cave Creek Valley, ♂, 4 ♀, Jan. 1956, M. Hite (FSCA); Devil's Den State Park, Devil's Kitchen Cave, juv. ♀, 9 September 1959, J. Tecklin (FSCA); Fayetteville, Mt. Kessler, 9 ♂, 18 ♀, 4 May 1955, N. B. Causey (FSCA); Ouachita Co., 5 mi. SW Camden, 2 ♂, 2 ♀, 1 January 1956, A. B. Jones (RLH). Randolph Co., 1 mi. N Pocahontas, ♂, 10 April 1936, L. Hubricht (RVC). Clay Co., Rector, 2 ♂, ♀, Dec. 1951, N. B. Causey (FSCA). Howard Co., sev. ♂, sev. ♀, 9 December 1953, L. Grey (FSCA). Union Co., Junction City, ♂, 3 ♀, 20 December 1952, N. B. Cau-

sey (FSCA). Columbia Co., Magnolia, 5 ♂, many ♀♀, 24 December 1949, N. B. Causey (FSCA). Polk Co., 5 N Scottsville, Pine-cedar-hardwood forest, ♀, 6 February 1955, B. Owen (FSCA).

Oklahoma: Sequoyah Co., Cottonwood Cave, ♂, 25 June 1970, J. H. Black (FSCA). Adair Co., Three Forks Cave between Stillwell and Bunch, juv. ♂, 26 January 1974, J. H. Black (FSCA).

Tennessee: Jefferson Co., Indian Cave near Jefferson City, 3 ♂, 2 ♀, 24 December 1924, J. D. Ives (FSCA); 5 ♂, 6 ♀, 12 February 1925, J. D. Ives (MCZ); and 3 ♂, 2 ♀, 18 April 1925, J. D. Ives (MCZ). Roane Co., Berry Cave, 5 ♂, 4 ♀, 10 July 1963, R. Brandon, J. Huheey (FSCA). DeKalb Co., Avant (Lindsay Williams) Cave, ♂, 23 December 1956, T. C. Barr (FSCA). Hamilton Co., Lookout, 2 ♂, 3 ♀, date unknown, Nathan Banks (MCZ).

Alabama: Madison Co., 4 mi. E Madison, Matthews Cave, 6 ♂, 18 ♀, 2 juvs., 22 August 1968, S. B. Peck (WAS). Colbert Co., McKinney Cave #2, 3 mi. W Sheffield, 2 ♂, 5 ♀, 19 December 1965, S. B. Peck (FSCA); and Murvel's Cave, 4 mi. NW Cherokee, ♂, 2 ♀, 19 December 1965, S. B. Peck (FSCA).

Mississippi: Jeff Davis Co., 3 mi. SSW Prentiss, near White Sand Cr., 2 ♂, 2 ♀, 25 December 1959, L. Hubricht (RLH). Franklin Co., 7 mi. W Meadville, 2 ♂, 5 ♀, 24 December 1954, N. B. Causey (FSCA).

Louisiana: Lincoln Par., Ruston, Pugh's Pond area, ♀, 10 March 1958, W. Harmon (FSCA). Tangipahoa Par., under rotting pine logs in open pine woods, 3 mi. SW Holton, 3 ♂, 4 ♀, 7 February 1966, K. A. Arnold (FSCA). Natchitoches Par., Creston, 2 ♂, 18 ♀, 22 February–5 March 1915, K. Schmidt (MCZ).

Cambala hubrichti Hoffman
Figs. 6, 11

Cambala annulata (nec Say, 1821) Loomis, 1938:37–38, fig. 11. Chamberlin and Hoffman, 1958:174.
Cambala hubrichti Hoffman, 1958:93–94.

Type locality.—Bluff along Doe River, 1 mile NW Hampton, Carter Co., Tennessee (Hoffman 1958).

Range (Fig. 11).—Southern Appalachian Mountains of southwestern Virginia, eastern Tennessee, and western North Carolina, from Wythe Co., Va., to the Nantahala Gorge, Swain Co., NC (Hoffman 1958). This can now be expanded to include the Black Mountains of NC (NCSM collection) and the Highlands Plateau of Macon Co., NC (one ♀ in Hoffman collection).

Remarks.—The illustration of the posterior gonopod by Loomis (1938, fig. 11b) is not entirely accurate. I have examined dozens of males and found that the anterior lobe of the coxa is not smoothly rounded but slightly acute

anteriodistad, and the posterior lobe is distinctly pointed on the anterior side rather than flattened.

Cambala ochra Chamberlin
Figs. 8, 12, 13

Cambala ochra Chamberlin, 1942:3, fig. 1. Chamberlin and Hoffman, 1958:175.
Cambala saltillona Chamberlin, 1943:3, figs. 1–2; 1952a:30. Chamberlin and Hoffman, 1958:175. NEW SYNONYMY.
Troglocambala loomisi Hoffman, 1956:10–11, figs. 9–11. NEW SYNONYMY.
Cambala loomisi Causey, 1964:237. Shear, 1969:135.

Type locality.—Darlington, St. Helena Par., Louisiana.

Range (Figs. 12, 13).—The distribution of *ochra,* based solely on male specimens, is from southern Indiana through central Kentucky, and the Cumberland Plateau region of Tennessee to the southern Gulf Coastal Plain, ranging westward into eastern Texas. It is sympatric in most of this area with *minor,* a fact which renders examination of the posterior gonopods of male cambaloids from their common range mandatory for identifications. Records of the latter species from Louisiana and the Cumberland Plateau by Causey (1959a, 1963) are unreliable and could well be *ochra* instead. In their common area of occurrence, *ochra* seems to be more abundant in the southern part and *minor,* in the northern part. The latter has a much broader range, however, being recorded from Arkansas, West Virginia, and Virginia, where *ochra* has not been encountered.

Remarks.—The type specimen of *ochra* is immature, and the anterior coxal lobe of the posterior gonopod is incompletely developed. However, the long basal stalk, typical of *saltillona* and *loomisi,* is present, and I therefore believe the three names to be synonymous, with *ochra* having priority. Collections of mature males from St. Helena Par., LA, can confirm this.

The configuration of the anterior coxal lobe of the posterior gonopod of *ochra* is more variable than in any other species of *Cambala*; the illustration (Fig. 8) is of the most common variant. In some males there is no distal hook, whereas in others it is more pronounced. Some specimens have a larger caudal projection than shown here, which is occasionally subequal to the anterior projection (in males having a reduced distal hook). No geographic pattern is evident to this variation, and, hence, there is no reason to recognize subspecies. The long basal stalk is common to all these variants and thus is the diagnostic feature of the species.

Cambala speobia (Chamberlin)
Figs. 9, 13

Eclytus (nec Holmgren, 1855) *speobius* Chamberlin, 1952a:11.
Eclomus speobius Chamberlin, 1952b:71. Chamberlin and Hoffman, 1958:175.
Cambala speobia Causey, 1964:243–244; 1971:273, figs. 1a, 2a.
Cambala caeca Loomis, 1953:417, figs. 1–3. Chamberlin and Hoffman, 1958:174.
Cambala captiosa Causey, 1959b:69–71, figs. 1–3.
Cambala reddelli reddelli Causey, 1964:239–241, figs. 1–4. NEW SYNONYMY.
Cambala reddelli inornatus Causey, 1964:241–242, fig. 5. NEW SYNONYMY.

Type locality.—Wyatt Cave, Sonora, Sutton Co., Texas (Chamberlin, 1952a). However Causey (1964) stated that Wyatt Cave was in adjacent Edwards Co. and not Sutton Co.

Range (Fig. 13).—Specimens have been examined from Williamson, Travis, Edwards, Culberson, and Wheeler cos., Texas, and the Edwards Plateau of Texas in general. Causey (1964) recorded it from 20 miles N Childress, Childress Co., Texas; and west of Cowles, San Miguel Co., and about 15 miles SW Cimarron, Colfax Co., New Mexico. Causey (1971) and Shear (1973) reported it from a cave in Coahuila State, Mexico. Two male cambaloids that resemble *speobia* in the configuration of the posterior gonopods have also been collected from Drain, Douglas Co., Oregon (AMNH).

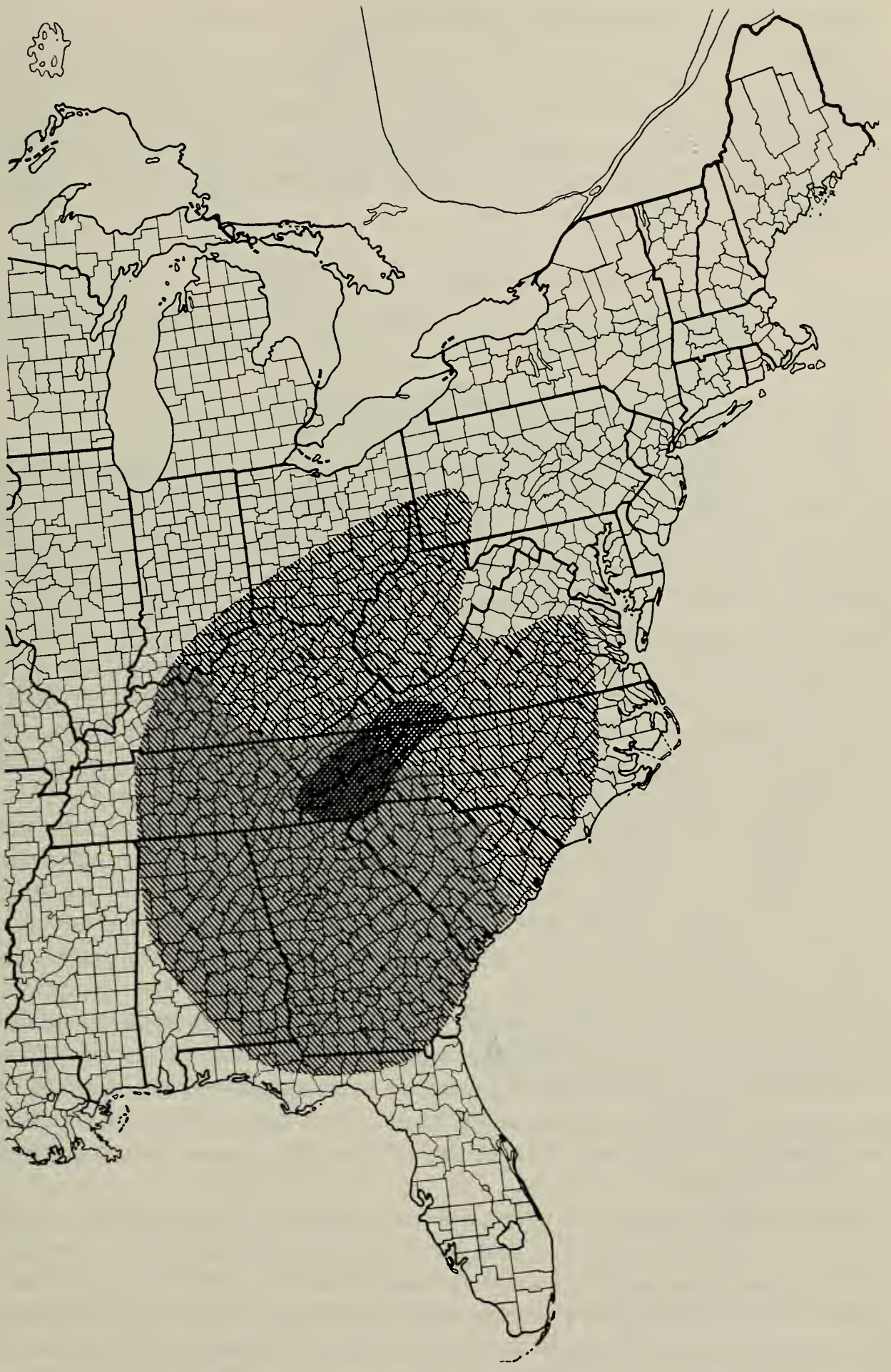
Remarks.—Causey (1964) transferred *speobius* into *Cambala* and synonymized *caeca* and *captiosa*. At the same time, however, she proposed two additional forms, *reddelli reddelli* and *reddelli inornatus*, which are virturally identical with the holotype of *speobia* and thus also synonyms. Moreover, I can find no significant differences between the two subspecies of *reddelli* and see no reason to distinguish the north Texas populations taxonomically.

Cambala texana Loomis
Figs. 10, 13

Cambala texana Loomis, 1938:40–41, fig. 13. Chamberlin and Hoffman, 1958:175.

→

Fig. 11. Distribution of *annulata* (diagonal lines) and *hubrichti* (cross hatched area). The shaded areas encompass all known, authentic records, including the range extremes in all directions.



Type locality.—Nacogdoches, Nacogdoches Co., Texas.

Range.—Known only from the type locality.

Remarks.—The illustrations by Loomis (1938), while accurate representations of the characters of the species, are not from the holotype, which was undissected when I received it. On the holotype, the uncate projection of the anterior coxal lobe of the posterior gonopod appears more strongly curved than in Loomis' illustration.

Cambala washingtonensis Causey

Cambala washingtonensis Causey, 1954:85, fig. 9. Chamberlin and Hoffman, 1958:175.

Type locality.—Wilma, Garfield Co., Washington.

Range.—Known only from type locality.

Remarks.—Causey (1954) described this as the "first western species of the genus" from a female, but Chamberlin and Hoffman (1958) noted that it was probably not congeneric with the eastern species of *Cambala*. In the description of *reddelli reddelli,* Causey (1964) stated that there is "very little difference between the gonopods of *C. reddelli* and *C. washingtonensis.*" Since to my knowledge no additional material of *washingtonensis* from the type locality has ever been collected, and the gonopods have certainly never been illustrated or described, it is a mystery how she knew their structure, much less that they were similar to those of *reddelli*. The wide geographic disparity between the two species would seem to render gonopodal similarity unlikely, especially when one notes the considerable differences between the gonopods of *ochra, speobia,* and *texana,* all of which occur relatively close together in Texas. In fact, the gonopods of *reddelli* are virtually identical to those of *speobia,* and if Causey's statement is accurate, *washingtonensis* must also fall as a synonym of *speobia*. One wonders if any gonopods of *washingtonensis* had been seen at the time this statement was made, and if so, why they were not illustrated to resolve the question of the generic position of this species. Additionally, Causey (1964) reported the range of *Cambala* as including "northern Idaho," but no specific Idaho records have ever been reported, and no such specimens are available in any museum collection. Consequently, one must assume that the basis for this citation of Idaho was the location of *washingtonensis* in an adjacent part of Washington.

Some insight into the *washingtonensis* problem is now possible due to the two male specimens of *Cambala* from Drain, Douglas Co., Oregon, which I discovered among unsorted material at the AMNH. As indicated earlier, the posterior gonopods are similar to those of *speobia,* suggesting that *washingtonensis* may indeed be a species of *Cambala* and a synonym of *speobia*. Unfortunately, Douglas Co. is in southwestern Oregon and sev-

Fig. 12. Distribution of *minor* (circles) and *ochra* (triangles).

eral hundred miles from Garfield Co., Washington, which is in the southeastern corner of that state. Hence, it would be risky to assume that the Oregon material is conspecific with that from the latter area, and the Oregon locality is reported merely for the sake of completion. Specific identification of this material should await collection of male topotypes of *washingtonensis*, but they do establish the presence of *Cambala* in the Pacific northwest. Causey (1964) may have been correct in stating that the gonopods of *washingtonensis* closely resemble those of *reddelli* (which would make *washingtonensis* a synonym of *speobia*), but the basis for this statement is obscure since the type and only reported specimen is a female. As noted in the introduction, the type of *washingtonensis* is absent from its published repository, the AMNH, so I was unable to examine it personally, and no

material identified as *washingtonensis* was found in the Causey collection (now at FSCA).

A Note on the Occurrence of *Cambala* in Caves

Perhaps the most intriguing aspect of the biology of *Cambala* is the occurrence of many of its species in caves. To date, *hubrichti, texana,* and *washingtonensis,* the last two known only from their type localities, have never been reported from a subterranean habitat, and I can now remove *hubrichti* from this list. During a recent survey of North Carolina caves by personnel of the NCSM, males and females of *hubrichti* were collected from caves in McDowell, Polk, Rutherford, and Transylvania cos. Specimens were found in the dark zone of Bat Cave, Rutherford Co., and the aphotic zone of Limekin Cave, McDowell Co. To the best of my knowledge, this is also the first report of cave millipeds from North Carolina.

The other species of *Cambala* commonly inhabit caves. The type species, which is distinct enough to render reliability to literature records, has been reported from caves in Alabama and Florida (Loomis 1943) and Tennessee (Causey 1959a). To these can now be added Wyandotte Cave, Crawford Co., Indiana (one male in MCZ collection) and Carter Cave, Robertson Co., Kentucky (one male in FSCA collection). Causey (1959a) reported *minor* as well as *annulata* from several Tennessee caves, but some of these records may be for *ochra* instead. Most specimens of "*minor*" were found on bat, cave rat, or raccoon dung in moist areas in the caves. She recognized three groups of cave millipeds in Tennessee—accidental species, including *annulata,* "epigean species that are somewhat tolerant of cave conditions" and hence occur there more often than those in the first category, and troglobites. *Cambala minor* was included in the second group. In a paper on cave millipeds of Missouri, Causey (1960) noted the wide geographic distribution of *minor* and suggested that it probably occurred in many caves of that state. This prediction is confirmed herein, as male specimens of *minor* have been examined from caves in Perry and Taney cos., Missouri.

Due to the confused nomenclature of *minor,* only a few cave records of *ochra* exist which can be considered reliable. One, involving the type material of *Troglocambala loomisi,* a synonym of *ochra,* is from Turk's (Brooklyn) Cave, Conecuh Co., Alabama.

Shear (1969) noted the identity problem with many cave records of *minor* and classified both *minor* and *annulata* as being troglophilic, *e.g.,* animals that occur in caves and can complete their life cycle there, but lack modifications for this life and also live in epigean habitats. This conforms to the second of Causey's (1959a) categories, and the two authors differ in the position of *annulata*. Shear also suggested that *speobia* in Texas may be a true troglobite, *e.g.,* an animal occurring solely underground, usually with

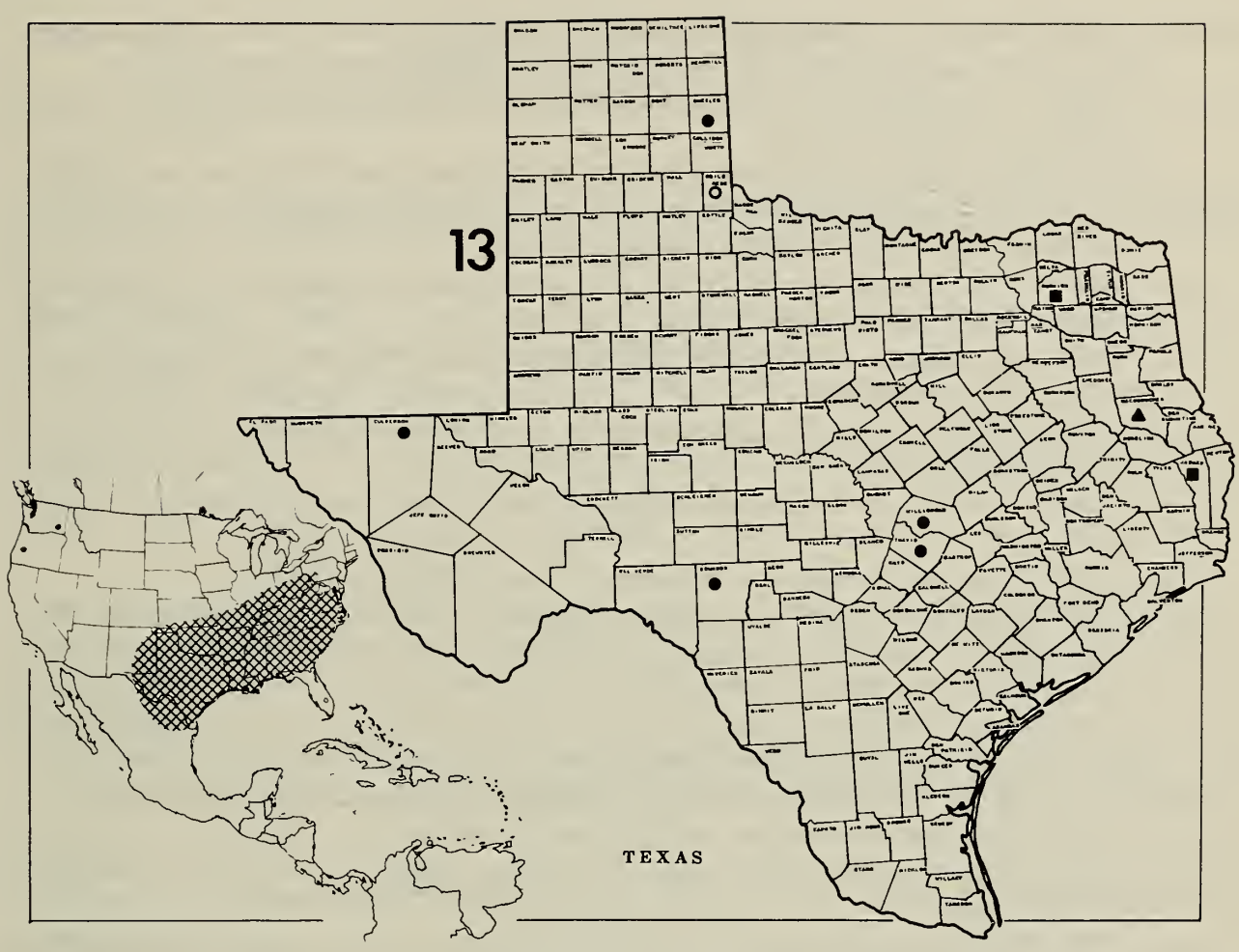


Fig. 13. Distribution of *speobia* (circles), *texana* (triangle), and *ochra* (squares) in Texas; the open symbol indicates a literature record believed to be valid. On the inset map, a smooth curve has been drawn around all records of *Cambala* to show the generic range. Oklahoma and southern Kansas are included even though no material has been collected from these states. The type locality of *washingtonensis* and that of the specimens from Oregon are shown in the northwest.

modifications for this life, and indeed this seems to be the case. All records of *speobia* or its synonyms known to me are from caves in Texas, New Mexico, and Mexico; the milliped has never been encountered in a surface habitat. Causey (1964, 1971) considered it a troglobite and noted the modified legs and antennae, and the absence of ocelli. Thus, although *annulata, minor, ochra,* and *speobia* all occur in caves, they are significantly different in the frequency of their occurrence there and the degree of their modification for subterranean life.

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